ECOLOGY LETTERS

Ecology Letters, (2017) **20**: 1405–1413 doi: 10.1111/ele.12848

LETTER

Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment

Juergen Kreyling,[1]* Jürgen Dengler,[2,3] Julia Walter,[4] Nikolay Velev,[5] Emin Ugurlu,[6] Desislava Sopotlieva,[5] Johannes Ransijn,[7] Catherine Picon-Cochard,[8] Ivan Nijs,[9] Pauline Hernandez,[8] Behlül Güler,[10] Philipp von Gillhaussen,[7] Hans J. De Boeck,[9] Juliette M.G. Bloor,[8] Sigi Berwaers,[9] Carl Beierkuhnlein,[11] Mohammed A.S. Arfin Khan,[7,12] Iva Apostolova,[5] Yasin Altan,[10] Michaela Zeiter,[13,14] Camilla Wellstein,[15] Marcelo Sternberg,[16] Andreas Stampfli,[13] Giandiego Campetella,[17] Sándor Bartha,[18,19] Michael Bahn,[20] and Anke Jentsch[7]

Abstract

Biodiversity can buffer ecosystem functioning against extreme climatic events, but few experiments have explicitly tested this. Here, we present the first multisite biodiversity × drought manipulation experiment to examine drought resistance and recovery at five temperate and Mediterranean grassland sites. Aboveground biomass production declined by 30% due to experimental drought (standardised local extremity by rainfall exclusion for 72–98 consecutive days). Species richness did not affect resistance but promoted recovery. Recovery was only positively affected by species richness in low-productive communities, with most diverse communities even showing overcompensation. This positive diversity effect could be linked to asynchrony of species responses. Our results suggest that a more context-dependent view considering the nature of the climatic disturbance as well as the productivity of the studied system will help identify under which circumstances biodiversity promotes drought resistance or recovery. Stability of biomass production can generally be expected to decrease with biodiversity loss and climate change.

Keywords

Asynchrony, diversity–stability relationship, resilience, insurance hypothesis, extreme event ecology, coordinated distributed experiment.

Ecology Letters (2017) **20**: 1405–1413

INTRODUCTION

Loss of biodiversity (Butchart *et al.* 2010) and climate change (e.g. via increasing frequency and magnitude of extreme climatic events; Schär *et al.* 2004; IPCC 2013) can both adversely affect ecosystem functioning (e.g. Cardinale *et al.* 2012; Reichstein *et al.* 2013). The role of biodiversity for the stability of ecosystem functioning in the face of climatic disturbance is therefore of utmost importance.

Resistance (*sensu* Pimm 1984) and recovery (*sensu* Hodgson *et al.* 2015) are two important facets of ecological stability (Pimm 1984; Hodgson *et al.* 2015; Donohue *et al.* 2016). Studies which have empirically evaluated diversity effects on these two facets of the stability of ecosystems subjected to extreme climatic events, however, report mixed results. Species richness may increase (Tilman & Downing 1994; Mulder *et al.* 2001; Kahmen *et al.* 2005; Isbell *et al.* 2015), not affect (Wardle *et al.* 2000; Pfisterer & Schmid 2002; Caldeira *et al.* 2005; Kahmen *et al.* 2005; DeClerck *et al.* 2006; Wang *et al.* 2007; van Ruijven & Berendse 2010) or even decrease (Pfisterer & Schmid 2002; Allison 2004; Vogel *et al.* 2012) ecosystem resistance. Here, we consider resistance as the lack of

---

[1] *Experimental Plant Ecology, Ernst-Moritz-Arndt University Greifswald, D-17487 Greifswald, Germany*
[2] *Plant Ecology, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany*
[3] *German Centre for Integrative Biodiversity Research (iDiv), 04103 Leipzig, Germany*
[4] *Landscape Ecology, University of Hohenheim, 70599 Stuttgart, Germany*
[5] *Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 1113 Sofia, Bulgaria*
[6] *Forest Engineering, Faculty of Forestry, Bursa Technical University, 152 Evler Str., No:2/10, 16330 Yildirim, Bursa, Turkey*
[7] *Disturbance Ecology, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany*
[8] *Grassland Ecosystem Research, UMR0874 INRA, VetAgroSup, 63000 Clermont-Ferrand, France*
[9] *Plants and Ecosystems, Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium*
[10] *Department of Biology, Faculty of Science & Letters, Manisa Celal Bayar University, Prof. Dr. Şehit İlhan Varank Campus, 45040 Yunusemre, Manisa, Turkey*
[11] *Biogeography, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany*
[12] *Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet 3114, Bangladesh*
[13] *School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, CH-3052 Zollikofen, Switzerland*
[14] *Institute of Plant Sciences, University of Bern, CH-3013 Bern, Switzerland*
[15] *Faculty of Science and Technology, Free University of Bozen, I-39100 Bozen, Italy*
[16] *School of Plant Sciences and Food Security, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel*
[17] *School of Biosciences and Veterinary Medicine, Plant Diversity and Ecosystems Management unit, University of Camerino, Camerino, Italy*
[18] *Institute of Ecology and Botany, MTA Centre for Ecological Research, H-2163 Vácrátót, Hungary*
[19] *School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley WE 6009, Australia*
[20] *Institute of Ecology, University of Innsbruck, A-6020 Innsbruck, Austria*
Correspondence: E-mail: juergen.kreyling@uni-greifswald.de

instantaneous impact of exogenous disturbance on a system (Hodgson *et al.* 2015) or, more explicitly, the degree to which ecosystem productivity remains unchanged. Likewise, species richness has been found to increase (Allison 2004; DeClerck *et al.* 2006; Vogel *et al.* 2012), decrease (Pfisterer & Schmid 2002) or have no effect (Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015) on recovery. Here, recovery is understood as the endogenous processes that pull the disturbed system back towards an equilibrium (Hodgson *et al.* 2015), or the degree to which ecosystem characteristics return to control or pre-disturbance levels after a disturbance. These mixed findings go beyond simple methodological differences among studies (e.g. artificial vs. natural communities; Wardle & Palmer 2016) and call for a better understanding of the biotic and abiotic conditions that affect the biodiversity–stability relationship within ecosystems.

Positive effects of biodiversity on ecosystem functioning have previously been attributed to selection effects or complementarity (Tilman *et al.* 1997; Loreau & Hector 2001). In addition, more diverse systems are expected to be more stable against perturbations and extreme events (*sensu* the Insurance Hypothesis, Yachi & Loreau 1999). Complementarity of species' responses to extreme events can induce such an insurance, that is improve stability in more diverse communities (Isbell *et al.* 2009; Loreau & de Mazancourt 2013; de Mazancourt *et al.* 2013; Gross *et al.* 2014). However, functional group diversity may be another important driver of ecosystem functioning (Tilman *et al.* 2007). For example, presence of key functional groups, such as legumes in grasslands, which are known to overproportionally affect biomass production (Spehn *et al.* 2002), also have the potential to modulate drought responses of coexisting species (Arfin Khan *et al.* 2014).

Experiments manipulating both biodiversity and extreme events are ideally suited to test for resistance to and recovery from disturbance, because they control for confounding effects by the direct comparison between experimentally induced climatic treatments and the control. Such experimental designs can be particularly useful to analyse non-equilibrium systems as they do not depend on metrics of ecological stability that relate performance after disturbance to performance before disturbance (e.g. Lloret *et al.* 2011; Isbell *et al.* 2015). Controlled experiments minimise noise due to temporal effects such as inherent micro-successional dynamics or weather dynamics. Furthermore, coordinated distributed experiments (Fraser *et al.* 2013) which consist of identical set-ups at multiple sites have the advantage of allowing biodiversity effects to be disentangled from effects of climatic disturbance in the bioclimatic context of different sites.

Here, we present results from the first coordinated distributed biodiversity experiment testing for interactions between different components of biodiversity and drought on model grassland systems across a continental biogeographic and climatic gradient. We examined the resistance and recovery of aboveground biomass production after prolonged drought across five sites in Europe and the Near East in field mesocosms. This unique set-up allowed us to test for the generality of observed effects. We expected that the drought resistance of biomass production would increase with increasing biodiversity irrespective of biotic (e.g. plant species composition, soil biotic community, productivity) and abiotic (e.g. climate, soil substrate) site conditions. Similarly, we also expected improved recovery with increasing biodiversity across sites in the year after the drought. Biodiversity, here, comprised species richness, functional group richness and presence of key functional groups such as legumes.

MATERIAL AND METHODS

Experimental design

An *in situ*-coordinated biodiversity × drought experiment was implemented using buried field mesocosms at five sites across Europe and the Near East (BE: Belgium, BG: Bulgaria, DE: Germany, FR: France, TR: Turkey; Table 1). At each of the five sites, grassland communities were planted at three species richness levels (1/3/6), also systematically altering functional group richness (FGR: 1/2/3) and the presence of legumes. Twelve locally frequent, native species which naturally occur together on the local target substrate were selected from the local species pool at each site. Study species included three functional groups (forbs, grasses, legumes) with four species representing each functional group per site (Table S1) and comprised different ecological strategy types at each site (Table S1). FGR was nested within species richness, so that its effects could be statistically tested (Scherer-Lorenzen 2008; Table S2). Per site and diversity level, 12 different species compositions were created (considered as replicates for the species richness levels). Each of these 180 unique species compositions (5 sites × 3 species richness levels × 12 species compositions) was set up once in the control and once in the drought treatment. All plants were grown from seed under standardised conditions at each site and planted into field mesocosms in early spring 2014 (> 3 months before the start of the drought manipulation). Seeds were collected from autochthonous populations close to the study sites (relying on expert knowledge).

Table 1 Site characteristics. Mean annual temperature (MAT) and mean annual precipitation (MAP) from www.worldclim.org (Hijmans *et al.* 2005)

Site	Country	Latitude (°)	Longitude (°)	Altitude (m a.s.l.)	MAT (°C)	MAP (mm)	Start of drought	Duration (days)
BE	Belgium	51.24917	4.6717	13	9.9	792	19.06.2014	88
BG	Bulgaria	42.6468	23.2981	650	10.1	597	23.06.2014	85
DE	Germany	49.9219	11.5819	365	8.0	674	25.06.2014	76
FR	France	45.7191	3.0166	890	9.7	687	15.07.2014	72
TR	Turkey	38.6765	27.3010	70	15.4	725	05.02.2015	98

Drought duration was standardised to local precipitation series to be comparable across sites (see text for details).

Each mesocosm consisted of a PVC tube of 30 cm diameter and 50 cm height. The base of mesocosms was closed with root matting, permeable for water but impermeable for roots. Mesocosms were buried in the soil to ensure natural temperature and drainage patterns, and filled with local soil substrate (homogenised, sieved to 2 cm). Mesocosms were planted with 18 pre-grown plant individuals in a systematic arrangement, avoiding conspecific neighbours, and ensuring that edge/centre ratios were similar for each species. Each species occurred at comparable frequencies within each species richness level. Non-target species were weeded out at a monthly interval. No fertilisation was applied. Upon planting, plants were cut to a height of 6 cm above ground level as standardisation. Mortality was checked regularly, and dead individuals were replaced during the first month after planting.

Drought manipulations

We simulated a pulsed-drought event using rain-out shelters with 100% rainfall reduction for specific periods during the local growing season. A randomised block design was applied at each site with two or three blocks (with each block containing both a rain-out shelter and a control). Mesocosms were completely randomised within each drought treatment-block combination, with each single species composition occurring twice (i.e. once per treatment). Drought length was standardised across sites and intended to be extreme on the basis that such events will become common in the future (Schär *et al.* 2004). Drought length was calculated for each site as 150% of the statistical 1000-year recurrence of consecutive days with < 2.5 mm precipitation based on local precipitation series in daily resolution (median series length: 30 years), and constrained within the local growing season (months with mean temperature > 5 °C and precipitation sum [mm] $> 2 \times$ mean temperature [°C]). Thus, the extremity of the manipulation is directly comparable for all sites. Ecologically, this is a more meaningful standardisation of drought length than simply applying the same drought length to systems under different climatic conditions and, consequentially, different evolutionary adaptation of species and plant traits. The drought treatment started after the second fifth of the growing season (see Table 1 for dates and duration per site). In case of natural drought outside the drought manipulation period, all mesocosms were irrigated to avoid drought stress (DE: 7×10 mm; FR: 16×10 mm; TR: 5×10 mm). In case of natural drought during the manipulation period, control plots were irrigated (DE: 4×10 mm; FR: 15×10 mm; TR: 4×10 mm). The drought manipulations were ended by irrigating the droughted mesocosms with 20 mm and the control mesocosms with 5 mm, to ensure a temporal synchrony between the post-manipulation rainfall events.

Biomass production

Aboveground biomass (B) was harvested at four dates during the experiment: (B_0) two weeks before the start of the drought treatment ('before drought'), to allow for a standardised quantification of biomass production during the drought period; (B_1) directly at the end of drought ('end of drought'); (B_2) at the end of the first growing season [except for TR, where (B_1) and (B_2) were identical and BG where no regrowth was observed between (B_1) and (B_2)]; (B_3) at peak biomass in the following growing season ('peak following year', used for assessing recovery after drought). Note that low values for this harvest in TR are explained by harvesting midway through the growing season as peak biomass in this Mediterranean system usually occurs at the end of the growing season, whereas peak biomass in temperate systems usually occurs in the middle of the growing season. Biomass was always harvested at 3 cm above ground, and included all plant material rooted inside the mesocosms. Species-specific biomass harvests were conducted directly after the drought (harvest B_1) and at the peak of the following year (harvest B_3; BG and DE only). Community biomass harvests were conducted at all other points in time (B_0, B_2).

Facets of ecological stability

We used relative measures of resistance and recovery to infer different facets of ecological stability (Pimm 1984; Donohue *et al.* 2016). Both metrics are dimensionless, and thus directly comparable between sites and communities with different levels of productivity. Within each experimental site and block, the single different species compositions occurred both under control and drought treatment. Consequently, we calculated resistance and recovery to drought for each unique species composition by comparing biomass production between drought treatment and control as:

$$Resistance = \frac{(B_1)_{Drought}}{(B_1)_{Control}}$$

$$Recovery = \frac{(B_3)_{Drought}}{(B_3)_{Control}}$$

where (B_1) is the biomass of each community at the end of the drought period and (B_3) is the biomass of each community at the peak of biomass production in the following year. The resistance index equals 1 for complete resistance and 0 for no resistance (no biomass production during drought). The recovery index equals 1 for complete recovery and is < 1 for incomplete recovery. Values > 1 indicate overcompensation. Community compositions with < 1.5 g dry weight per mesocosm under control conditions (3% of all cases) were disregarded because of their high relative uncertainty (e.g. incremental differences in cutting height can have strong relative effects) and their potential to overproportionally inflate errors (grand mean over all measurements is 37.2 ± 2.9 (SE) g per mesocosm).

Statistical analyses

We used linear mixed-effects models to test whether biomass production for each single time step (from harvest to harvest) depended on 'species richness' and 'drought' treatments (testing for main effects and their interaction; Fig. 1). The blocked structure of the experimental design was acknowledged by nesting 'blocks' within 'sites' in the formulation of the random effects.

Resistance and recovery to drought were tested with similarly structured mixed models with the fixed-effects 'species

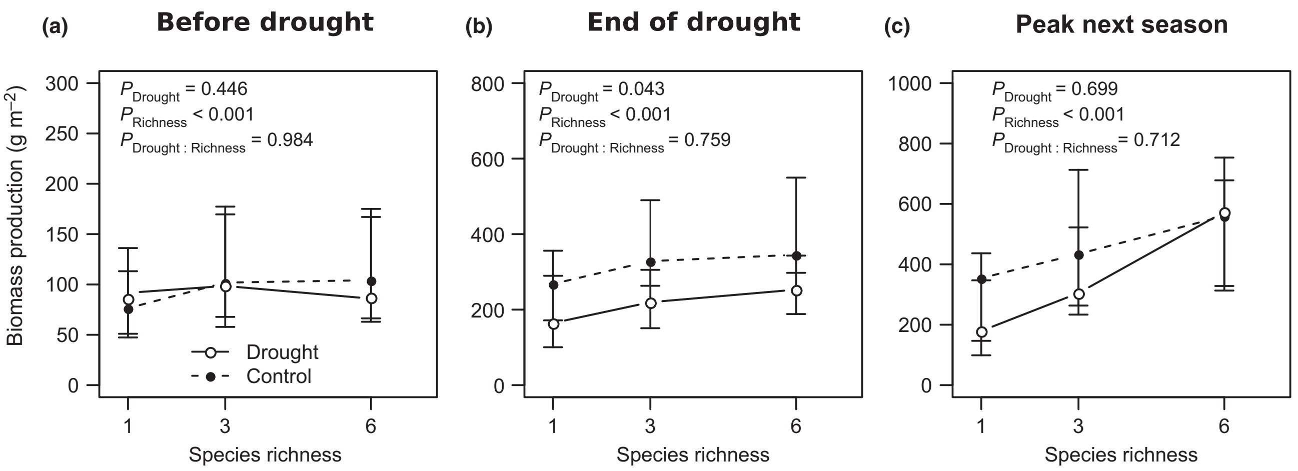

Figure 1 Biomass production across sites (median and quartiles, $n = 60$ per point) between the previous and the specified time step. Fixed effects from mixed-model ANOVA are given. Site-specific biomass production is provided in Fig. S1. Note that 'before drought' and 'end-of-drought' data stem from the same year; their sum being equivalent to the harvest at peak next season in terms of time covered per growing season.

richness', 'productivity under control conditions' and their interaction combined with the same formulation of random effects as described above (Fig. 2). 'Species richness' was introduced into the model as linear numeric variable, but note that log-linear and factorial response produced qualitatively the same results in all models. 'Productivity under control conditions' (B_1 for resistance and B_3 for recovery) was also analysed as linear numeric variable (again, log-linear response did not affect the outcome). For further visualisation, communities were subsequently separated into low productive and high productive using the respective 70% percentile as split (400 g m^{-2} control biomass for resistance and 700 g m^{-2} control biomass for recovery, respectively; Fig. 2c–f).

A second model formulation was used to test also for the effects of 'FGR' and 'presence of legumes' on resistance and recovery, by adding both terms as fixed effects after the fixed-effect 'species richness' and the same random-effect formulation as described above (Table 2). For all models, the response variable was log(x + 1.1)-transformed (Hector *et al.* 2002) to meet model assumptions (homoscedasticity and normal distribution of residuals). Models were fit with the lmer function in the lme4 package (version 1.1-12) in R (R Core Team 2016), and results were extracted with the ANOVA function in the lmer.test package (version 2.0-33) in R.

Observed diversity effects were partitioned into complementarity effects and selection effects according to Loreau & Hector (2001). This partitioning was performed by the addpart function in the package pdiv (version 1.4.1) in R and provides these effects in original units of the response parameter (here: g biomass per area). Further statistical analysis of complementarity and selection effects was performed using mixed-effects models as described above for biomass production.

Asynchrony in species responses to drought was assessed according to Loreau & de Mazancourt (2008) as 1—the degree of synchrony in species biomass production between control and drought treatment for each species composition, that is comparing changes in biomass between treatment and control, which do not have a temporal component. Specifically, community-level variances within each species composition and treatment were compared to species-level variance of the same species composition between the treatments (drought vs. control), resulting in one value for each species composition. Asynchrony ranges from 0 (perfect synchrony) to 1 (perfect asynchrony). Synchrony was extracted by the synchrony function of the package codyn (version 1.1.0) in R. Further statistical analysis on asynchrony values was performed by mixed-effects models as described above for biomass production. As species-specific biomass data were not available for all sites and times, two separate models were applied, one over all sites for harvest B_1 ('end of drought') with site and species richness as fixed effects, and another one for BG and DE only for harvests B_1 and B_3 ('peak next season') with harvest year, site and species richness as fixed effects. Note that species asynchrony increases (as we use 1 - synchrony) with species richness (Loreau & de Mazancourt 2008). These authors show that, in the special case of independent species responses, synchrony should decline by 1/S, which approximately fits for our data. Therefore, we focus the interpretation of our data on site differences and changes in asynchrony from the event year to the year after the event.

RESULTS

Species richness increased biomass production irrespective of measurement date (Fig. 1). Drought reduced biomass production by 30% on average across diversity treatments and sites (Fig. 1b). Species richness had no significant effect on drought resistance of biomass production ($P = 0.580$; Fig. 2a). Overall, recovery values showed that the most species-rich communities (six species) overcompensated for biomass reduction recorded during the drought period (mean recovery = 1.19 ± 0.10 (SE)). In contrast, monocultures and low-diversity communities (three species) only reached recovery values of 0.85 ± 0.07 and 0.82 ± 0.10, respectively, within 1 year after the experimental drought ($P = 0.002$; Fig. 2b).

Observed recovery effects were driven by productivity (interaction between species richness and productivity: $P = 0.014$; Fig. 2b). The richness effect on recovery was only significant

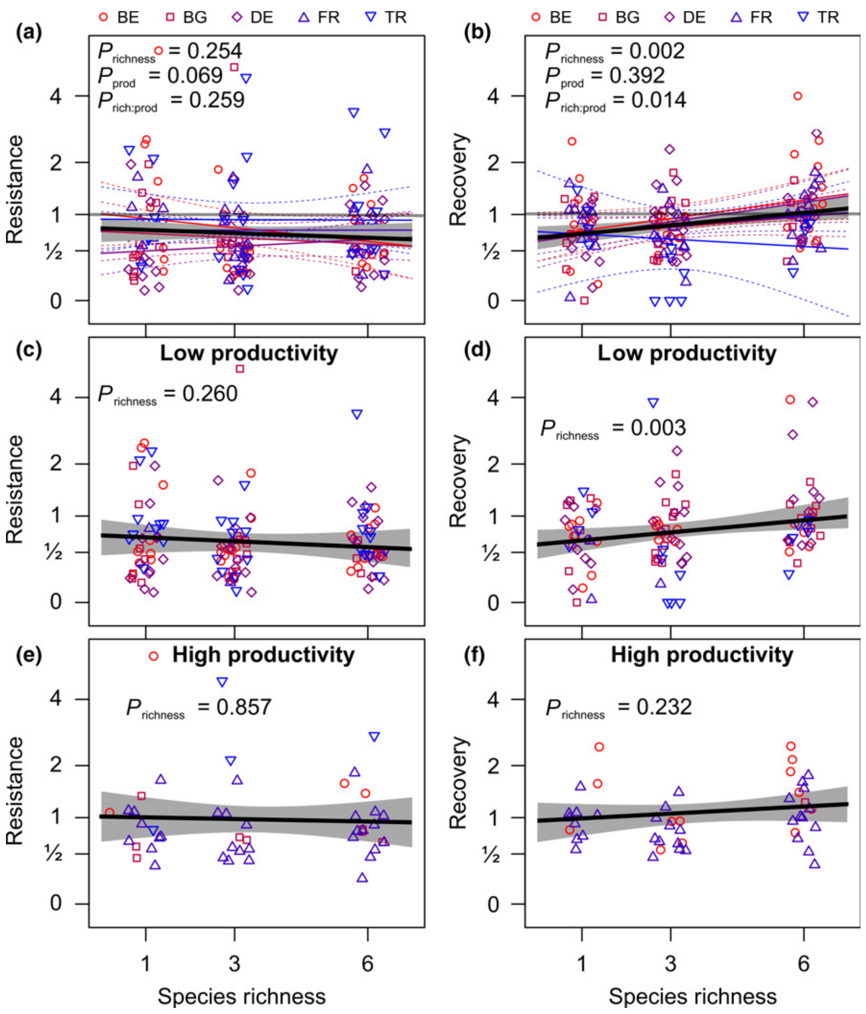

Figure 2 Species richness effects on resistance and recovery to drought. Species richness did not affect resistance (i.e. the biomass ratio between drought manipulation and control at the end of drought) (a), irrespective of community productivity (tested as numeric explanatory parameter in (a) and further visualised here as low productivity (< 400 g m^{-2} = 0.7-quantile; (c)) and high productivity (> 400 g m^{-2} (e))). Species richness affected recovery (i.e. the biomass ratio between drought manipulation and control 1 year after the drought (b)), but this effect depended on productivity (significant interaction in (a)), further visualised by separating into low (i.e. communities with a productivity of < 700 g m^{-2} (= 0.7-quantile) in the year after the drought manipulation) and high productivity plots (f) (i.e. communities with a productivity of > 700 g m^{-2}). Black solid lines are mixed-effects model fits, and grey shades represent their respective 95% confidence intervals. *P*-values are given for the fixed species richness effect, the fixed productivity effect (P_{prod}) and their interaction ($P_{\text{rich : prod}}$) in (a) and (b). Values on the *y*-axis are unitless. *x*-axis values are jittered around the applied levels of species richness to improve visibility of single points ($n = 12$ per site and species richness level in (a) and (b)). Colours and symbols code the single sites with their respective linear model fits (solid lines) and 95% confidence intervals (dotted lines). Note that no single-site linear model yielded statistical significance. Grey horizontal lines represent complete resistance (a) and recovery (b). For the latter, values above 1 represent overcompensation.

for low-productive communities (Fig. 2d) but not for high-productive communities (Fig. 2f). No such productivity-dependent differentiation was observed for resistance (Fig. 2c, e). Neither functional group richness nor presence of legumes had a significant effect on resistance or recovery (Table 2).

The positive richness effect on recovery after drought appeared to be driven by asynchrony of species responses to drought. Asynchrony in species performance between drought and control increased from the end of the drought to the peak biomass of the following year (year: $P = 0.002$; Fig. 3). Asynchrony did not differ between sites (both models with no significant site effect or any interaction with site).

Complementarity had a greater influence on observed diversity effects on aboveground biomass production compared with selection effects (Fig. 4). Drought reduced the magnitude of these complementarity effects on the end-of-drought harvest ($P < 0.001$). Higher species richness (six vs. three species) tended to increase complementarity in both harvests ($P = 0.051$ and 0.058, respectively) while it reduced the (already negative) selection effect in the harvest one year after the drought ($P = 0.008$). The selection effect was not affected by the drought treatment (Table 2).

DISCUSSION

Species richness improved the drought recovery of biomass production in our multisite experiment. This positive richness effect was driven by community productivity. Recovery was

Table 2 Biodiversity parameters affecting the resistance and recovery of biomass production in response to drought periods

Fixed effects	Resistance	Recovery
Species richness	$F_{156.8} = 1.11^{0.293}$	$\boldsymbol{F_{136.5} = 6.67^{0.011}}$
Legume presence	$F_{154.8} = 2.13^{0.146}$	$F_{135.9} = 0.40^{0.524}$
Functional group richness	$F_{157.4} = 0.01^{0.922}$	$F_{136.5} = 0.36^{0.528}$

Results are from mixed-model ANOVA with the single species compositions nested in treatment blocks further nested in study site as random effects. Both response variables were log(x + 1.1)-transformed. Satterthwaite approximation is given for denominator degrees of freedom. Superscripts represent the respective *P*-values, Bold if significant at $p < 0.05$.

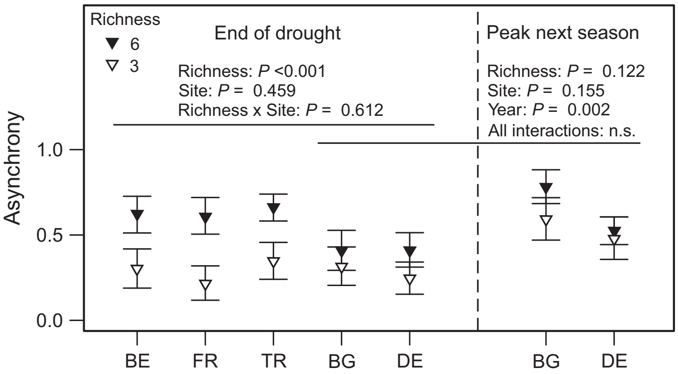

Figure 3 Asynchrony in species responses to the drought manipulation (mean ± SEM, $n = 12$ per point) expressed as 1 - synchrony according to Loreau & de Mazancourt (2008) between species variances in control and drought manipulation at the end of the drought period and at peak biomass in the following year. Asynchrony ranges from 0 (perfect synchrony) to 1 (perfect asynchrony). ANOVA results are given for two subsets: (i) all sites at the end of the drought period and (ii) sites BG and DE at both points in time (subsets are indicated by the solid horizontal lines below each ANOVA result). Species asynchrony being higher in more diverse than in less diverse communities is an inherent effect of the index, which increases (as we use 1 - synchrony) with species richness (Loreau & de Mazancourt 2008). These authors show that, in the special case of independent species responses, synchrony should decline by 1/S, which approximately fits for our data for end of drought. Based on this, the results emphasise (a) no significant difference in asynchrony among the five sites and (b) an increase in asynchrony from the event year to the year after the event.

high irrespective of species richness in our high-productive plots while it depended on species richness in the low-productive communities where only diverse communities reached full recovery within 1 year (Fig. 2d,f). This is consistent with the idea that conservative, slow-growing species characteristic of low-productivity communities are less able to take advantage of increased resource availability after the end of the drought (Lepš *et al.* 1982; Grime *et al.* 2000; Májeková *et al.* 2014; Reich 2014). Our species pool covered a wide gradient of plant strategy types, including slow- and also fast-growing species and productivity levels ranged from 2 g m^{-2} to 7 kg m^{-2} (peak biomass in control plots in the second study year, 1st quartile: 165 g m^{-2}, median: 435 g m^{-2}, 3rd quartile: 897 g m^{-2}). Taken together, the advantages of high species richness (and an increased range in species traits) may be greater for recovery of biomass production after drought where productivity is low.

Community productivity has been reported to negatively affect resistance to drought irrespective of species richness (Wang *et al.* 2007). Furthermore, van Ruijven & Berendse (2010) show that a positive diversity resistance effect to a natural drought depends negatively on productivity, while recovery after drought increases with diversity independent of productivity. The positive effect of species richness on recovery, at least in low-productive communities, observed in the present study is generally consistent with previous studies showing a positive relationship between diversity and recovery after extreme events (Allison 2004; DeClerck *et al.* 2006; van Ruijven & Berendse 2010; Vogel *et al.* 2012). In contrast with some previous grassland studies (e.g. Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015), we did not observe significant diversity effects on resistance of biomass production across sites. This may be due to our short gradient in species richness (1–6 species). Meta-analyses on biodiversity–stability and biodiversity–ecosystem functioning studies, however, show strongest diversity effects right in the range of species richness covered by our experiment (Cardinale *et al.* 2006; Isbell *et al.* 2015). Species resistance to sudden pulse events (our study) may be different compared with chronic press events such as prolonged natural drought events (e.g. Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015) which usually include small rainfall events even during the dry periods (Knapp *et al.* 2016). The latter offer greater options for community resistance through asynchrony of species responses, promoting subordinate and stress-tolerant species, which are usually less productive under regular climatic conditions (Mariotte *et al.* 2013). Such a reordering of community dominance patterns, however, requires time and was not observed during our drought experiment (Fig. 3). Therefore, we suggest that biodiversity effects are more likely to occur after rather than during sudden pulse events, affecting recovery rather than resistance. This expectation is confirmed by increased asynchrony between drought and control over time following our experimental drought. It is noteworthy that the drought-induced reduction in biomass production in our study was comparable in effect size to severe natural drought events such as the Central European heat wave in summer 2003 (Ciais *et al.* 2005), as well as to other studies on diversity–stability relations (Pfisterer & Schmid 2002; van Ruijven & Berendse 2010; Isbell *et al.* 2015). Significant increase in senescence due to drought at all sites (Fig. S2) indicated drought stress for our plants.

Mixed results on diversity–stability (*sensu* Pimm 1984; Donohue *et al.* 2016) effects in the literature may generally reflect (i) characteristics of the climate extremes, (ii) characteristics of the studied communities and (iii) metrics of ecological stability.

(i) In addition to potential differences in diversity–stability effects among pulse and chronic events , the extremity of the event could affect the outcome. Drought duration defined by rainfall exclusion relative to local climate series should not be directly interpreted as evidence for extreme ecological drought effects (Smith 2011; Kreyling *et al.* 2017). Biodiversity–stability studies will benefit from objective and relative quantification of extremity (Smith 2011) and rigorous testing along gradients of extremity to uncover potential thresholds and nonlinearities (Kreyling *et al.* 2014).

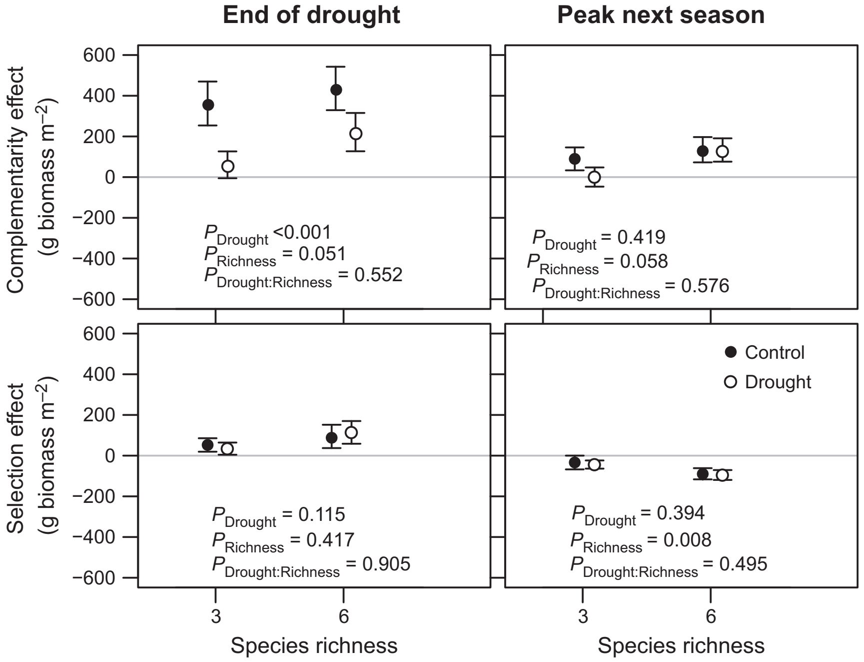

Figure 4 Partitioning the observed diversity effects into complementarity and selection effects according to Loreau & Hector (2001). Displayed are mean ± SEM for 'end-of-drought' harvests (all sites, $n = 60$) and for 'peak next season' harvests (BG and DE only, $n = 24$). Fixed effects from mixed-model ANOVA are given.

(ii) Characteristics of the target communities can affect biodiversity effects on resistance to and recovery from disturbance. Our data imply that such diversity effects depend on the productivity of the study systems. Furthermore, the successional state of ecosystems and age of individuals may also need to be taken into account when evaluating their response to climate extremes. It has been suggested that ecological stability of early-successional state plant communities is driven by recovery while stability of late-successional state communities is driven by resistance to drought (Lepš *et al.* 1982). Still, the importance of plant community age for the stability of grassland ecosystem processes remains unknown (Bloor & Bardgett 2012) and research focusing on undisturbed, late-successional ecosystems might consequently lead to an underestimation of instantaneous climate change impacts (Kröel-Dulay *et al.* 2015). Likewise, studies on young or recently disturbed ecosystems may overestimate direct impacts while emphasising potential for recovery. Studying such non-equilibrium systems further emphasises the need for controlled designs to allow for sound quantification of the drought resistance and recovery by directly comparing performance under drought and control conditions. Generally, diversity effects in controlled, artificially created and randomised species compositions might differ from effects of non-random species loss in nature (Wardle & Palmer 2016). This, however, does not explain the mixed results in biodiversity–stability studies as the vast majority of those studies artificially generated their communities.

(iii) Terminology on components of ecological stability, such as resilience, resistance and recovery, is ambiguous in the scientific literature (Holling 1973; Pimm 1984; Grimm & Wissel 1997; Hodgson *et al.* 2015; Donohue *et al.* 2016). Here, we focused on the ratio between biomass production in the drought treatment and control conditions for defined periods of time (the drought period for resistance and the year after drought for recovery), thereby obtaining more direct estimates of resistance and recovery than observational surveys, which rely on comparisons with previous years, and usually include biomass produced before or after the drought. Adapting stability indices commonly used in observational time series (Isbell *et al.* 2015) to our controlled design, we find no significant effects of species richness on resistance and resilience (Fig. S3). While the shifting baseline in a controlled design (control during the drought year vs. control after the drought year) controls for confounding effects in non-equilibrium systems, it also hampers direct comparisons to observational studies (see Appendix S3 for details). Still, the main difference to our recovery index is that the resilience index *sensu* Isbell *et al.* (2015) focuses only on stability and does not allow for a separation between overcompensation and incomplete recovery (see Appendix S3 for details). While this is a sound definition from the perspective of stability theory, we argue that overcompensation, as observed in our study, is of high ecological and economical importance.

Recovery in our most species-rich communities (6 species) indicated overcompensation of biomass production in the year following experimental drought. Asynchrony in species responses to the drought (compared with species performance under control conditions) increased from the end of the drought period, when species richness had no effect on resistance, through to the following year, when species richness resulted in the positive effect on recovery. This is consistent with the insurance hypothesis (Yachi & Loreau 1999), which states that more diverse communities are more likely to contain species with unique strategies to cope with perturbations.

It has been suggested that insurance effects may occur predominantly in the absence of positive diversity–productivity relationships before the perturbation (van Ruijven & Berendse 2003; Allison 2004). This was not the case in our study where a positive diversity–productivity relationship was observed both before and also at the end of the drought period and throughout the recovery period across sites. Positive effects of species richness on ecosystem functioning during recovery after drought can be explained by higher complementarity or resource partitioning associated with the nutrient flush caused by rewetting (with resource supply during the moment of rewetting having been greater for droughted than for non-droughted communities) (DeClerck *et al.* 2006; Bloor & Bardgett 2012; Roy *et al.* 2016).

Generally, our results confirm the positive biodiversity–ecosystem functioning relationship (e.g. Cardinale *et al.* 2012). Our coordinated, distributed experimental study suggests that species richness, but not functional group richness or presence of legumes, underlies these observed positive diversity effects (Table 2). Moreover, complementarity, rather than selection (*sensu* Loreau & Hector 2001), explained the positive diversity effects. Drought reduced the positive complementarity effect (Fig. 4), which is in agreement with recent findings from other grassland field studies (Craven *et al.* 2016). Contrary to expectations (Spehn *et al.* 2002; Arfin Khan *et al.* 2014), presence of legumes did not affect resistance to or recovery from drought.

Our study demonstrates that species richness has positive effects on ecosystem functioning by supporting recovery of biomass production after drought in low-productive, and presumably slow-growing, communities. The most diverse communities even overcompensated for the negative drought effect during recovery by reordering community composition, as indicated by increased asynchrony of species responses to drought. No diversity effect was found for resistance against pulsed, prolonged drought. We suggest that a more context-dependent view (e.g. considering pulsed vs. chronic events, extremity of the event, productivity and successional stage of the studied system) will help identify which circumstances promote drought resistance or recovery. Restoring and protecting biodiversity in times of increasing climatic extremity, nevertheless, can generally be expected to improve ecological stability, thereby ensuring ecosystem productivity and also productivity-dependent ecosystem services.

ACKNOWLEDGEMENTS

This work is part of the project SIGNAL which is funded by the ERA-Net BiodivERsA (http://www.biodiversa.org; Funding ID 01LC1201), with the national funders Belgian Federal Science Policy Office (BELSPO), German Federal Ministry of Education and Research (BMBF), Bulgarian Science Found and Ministère de l'Écologie, du Développement durable et de l'Énergie (France) as part of the 2011–2012 BiodivERsA call for research proposals. For site FR, we thank P. Pichon, A. Salcedo, J. Pottier, M.E. Lefranc, M. Michaux, A. Vernay and G. Zannin for help during the course of the experiment. We thank three anonymous referees for insightful and constructive comments on an earlier version of this manuscript.

AUTHORSHIP

AJ, CW and JK conceived the project; all authors developed the project at a workshop; JD, AJ and JK coordinated the experiment across sites; SB, HJDB and IN contributed experimental data for site BE; IA, DS and NV contributed experimental data for site BG; CB, JD, PvG, AJ, MASAK, JK, JR and JW contributed experimental data for site DE; CPC and PH contributed experimental data for site FR; YA, EU and BG contributed experimental data for site TR; JK assembled and analysed the data; and JK wrote the manuscript, with substantial input from JMGB and contributions from all authors.

DATA ACCESSIBILITY STATEMENT

Data supporting the results are archived at Dryad doi:10.5061/dryad.hb8r0.

REFERENCES

Allison, G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecol. Monogr.*, 74, 117–134.

Arfin Khan, M.A., Grant, K., Beierkuhnlein, C., Kreyling, J. & Jentsch, A. (2014). Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland. *Plant Soil*, 379, 161–175.

Bloor, J.M.G. & Bardgett, R.D. (2012). Stability of above-ground and belowground processes to extreme drought in model grassland ecosystems: interactions with plant species diversity and soil nitrogen availability. *Perspect. Plant Ecol.*, 14, 193–204.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W. & Almond, R.E.A., *et al.* (2010). Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.

Caldeira, M.C., Hector, A., Loreau, M. & Pereira, J.S. (2005). Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos*, 110, 115–123.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C. & Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., et al. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J. & Allard, V., *et al.* (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437, 529–533.

Craven, D., Isbell, F., Manning, P., Connolly, J., Bruelheide, H., Ebeling, A., *et al.* (2016). Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Philos. Trans. R. Soc. B Biol. Sci.*, 371, 0150277.

DeClerck, F.A.J., Barbour, M.G. & Sawyer, J.O. (2006). Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology*, 87, 2787–2799.

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L. & Fowler, M.S., *et al.* (2016). Navigating the complexity of ecological stability. *Ecol. Lett.*, 19, 1172–1185.

Fraser, L.H., Henry, H.A.L., Carlyle, D., White, S., Beierkuhnlein, C. & Cahill, J., *et al.* (2013). Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Front. Ecol. Environ.*, 11, 147–155.

Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., et al. (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science*, 289, 762–765.

Grimm, V. & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323–334.

Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M. & Polley, H.W., *et al*. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *Am. Nat*., 183, 1–12.

Hector, A., Bazeley-White, E., Loreau, M., Otway, S. & Schmid, B. (2002). Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett*., 5, 502–511.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol*., 25, 1965–1978.

Hodgson, D., McDonald, J.L. & Hosken, D.J. (2015). What do you mean, 'resilient'? *Trends Ecol. Evol*., 30, 503–506.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst*., 4, 1–23.

IPCC (ed.) (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY.

Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett*., 12, 443–451.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B. & Beierkuhnlein, C., *et al*. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.

Kahmen, A., Perner, J. & Buchmann, N. (2005). Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct. Ecol*., 19, 594–601.

Knapp, A.K., Avolio, M.L., Beier, C., Carroll, C.J.W., Collins, S.L. & Dukes, J.S., *et al*. (2016). Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. *Glob. Change Biol*., 23, 1774–1782.

Kreyling, J., Jentsch, A. & Beier, C. (2014). Beyond realism in climate change experiments: gradient approaches identify thresholds and tipping points. *Ecol. Lett*., 17, 125.

Kreyling, J., Arfin Khan, M.A.S., Sultana, F., Babel, W., Beierkuhnlein, C. & Foken, T., *et al*. (2017). Drought effects in climate change manipulation experiments: quantifying the influence of ambient weather conditions and rain-out shelter artifacts. *Ecosystems*, 20, 301–315.

Kröel-Dulay, G., Ransijn, J., Schmidt, I.K., Beier, C., de Angelis, P. & de Dato, G., *et al*. (2015). Increased sensitivity to climate change in disturbed ecosystems. *Nat. Comm*., 6, 6682.

Lepš, J., Osbornovakosinova, J. & Rejmanek, M. (1982). Community stability, complexity and species life-history strategies. *Vegetatio*, 50, 53–63.

Lloret, F., Keeling, E.G. & Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120, 1909–1920.

Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat*., 172, E48–E66.

Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett*., 16, 106–115.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.

Májeková, M., de Bello, F., Doležal, J. & Lepš, J. (2014). Plant functional traits as determinants of population stability. *Ecology*, 95, 2369–2374.

Mariotte, P., Vandenberghe, C., Kardol, P., Hagedorn, F. & Buttler, A. (2013). Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *J. Ecol*., 101, 763–773.

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., de Luca, E. & Grace, J.B., *et al*. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett*., 16, 617–625.

Mulder, C.P., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity-productivity relationships: the role of positive interactions. *Proc. Natl Acad. Sci. USA*, 98, 6704–6708.

Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84–86.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R version 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reich, P.B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol*., 102, 275–301.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D. & Seneviratne, S.I., *et al*. (2013). Climate extremes and the carbon cycle. *Nature*, 500, 287–295.

Roy, J., Picon-Cochard, C., Augusti, A., Benot, M.-L., Thiery, L. & Darsonville, O., *et al*. (2016). Elevated CO_2 maintains grassland net carbon uptake under a future heat and drought extreme. *Proc. Natl Acad. Sci. USA*, 113, 6224–6229.

van Ruijven, J. & Berendse, F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecol. Lett*., 6, 170–175.

van Ruijven, J. & Berendse, F. (2010). Diversity enhances community recovery, but not resistance, after drought. *J. Ecol*., 98, 81–86.

Schär, C., Vidale, P.L., Luthi, D., Frei, C., Haberli, C. & Liniger, M.A., *et al*. (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, 427, 332–336.

Scherer-Lorenzen, M. (2008). Functional diversity affects decomposition processes in experimental grasslands. *Funct. Ecol*., 22, 547–555.

Smith, M.D. (2011). An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol*., 99, 656–663.

Spehn, E.M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M.C. & Dimitrakopoulos, P.G., *et al*. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, 98, 205–218.

Tilman, D. & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature*, 367, 363–365.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci. USA*, 94, 1857–1861.

Tilman, D., Reich, P.B. & Knops, J. (2007). Ecology – diversity and stability in plant communities – reply. *Nature*, 446, E7–E8.

Vogel, A., Scherer-Lorenzen, M. & Weigelt, A. (2012). Grassland resistance and resilience after drought depends on management intensity and species richness. *PLoS ONE*, 7, e36992.

Wang, Y., Yu, S. & Wang, J. (2007). Biomass-dependent susceptibility to drought in experimental grassland communities. *Ecol. Lett*., 10, 401–410.

Wardle, D.A. & Palmer, M. (2016). Do experiments exploring plant diversity-ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *J. Veg. Sci*., 27, 646–653.

Wardle, D.A., Bonner, K.I. & Barker, G.M. (2000). Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos*, 89, 11–23.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA*, 96, 1463–1468.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Josep Penuelas
Manuscript received 11 July 2017
First decision made 6 August 2017
Manuscript accepted 14 August 2017